

XIII.—On the Development of *Arenicola piscatorum*; with Remarks upon that of other Branchiferous Annelides. By Dr. MAX SCHULTZE*.

[With a Plate.]

MOST of the Branchiferous Annelida, of which the earliest forms have yet been observed, leave the egg-capsule or the embryonic receptacle of the mother in a condition by which they are enabled to swim about freely. They are furnished with strong bands of cilia, or with a uniform ciliary coat, so that they can roll about in the water at pleasure.

By fishing with a fine net in the neighbourhood of the coast or on the high sea, a considerable number of such roving Annelidan larvæ come to the hands of the zoologist. As these, without exception, when in their earliest stages of development, possess a very different form from their parents, and are destitute of any organs by which the determination of their origin might be rendered possible, a long series of investigations upon their further evolution is necessary to obtain certain indications of their parentage. It is rarely that such larvæ can be kept alive in the experimental glasses long enough to enable us to follow their further metamorphoses upon one and the same individual. Naturalists have therefore generally been compelled to confine themselves to collecting the different young forms of the same animal one after the other, by repeated fishings, and uniting these to form a general picture of the development. Frequently however it happens that, notwithstanding constant exertions, a form once observed never again comes into the net, or occurs so rarely, that the origin of the single larvæ has remained unknown, whilst others which were taken plentifully and at different periods continued so obstinately in a certain early stage of development, that all endeavours to ascertain their subsequent fate were vain. It is therefore not to be wondered at if, amongst the great number of young Annelides which have been fished up from the sea and described, there are but few which we can refer to their parents. A remarkable example how, with the greatest perseverance, the goal is often reached only after the lapse of a long period, is furnished by the *Mesotrocha sexoculata*, recently ascertained by Max Müller to be the larva of *Chaetopterus*, although J. Müller and Busch were repeatedly led to investigate it during their excursions without being able to observe any considerable progress in its development.

The employment of artificial impregnation will be of importance to the study of the metamorphoses of the Annelida. As yet this has only been tried once by Quatrefages, who by this

* From the Abhandl. der naturforsch. Gesellsch. in Halle, vol. iv. Communicated by the Author and translated by W. S. Dallas, F.L.S. &c.

means obtained young *Hermellæ*, and was enabled to follow their development for a considerable time. When we possess a series of similar observations, the forms discovered swimming freely, whose mature state is still unknown, may be gradually determined. Thus, R. Leuckart remarks*, that the larvæ represented by Busch, 'Beobachtungen,' &c. tab. 7. figs. 5, 6, which were taken up from the open sea, remind one of the young *Hermellæ* just mentioned, by their long stiff bristles. But in this case it cannot be supposed that the former are actually the progeny of *Hermella*, as the latter, according to Quatrefages, lose their cilia before the appearance of any segmentation of the body.

Our knowledge of the development of the Annelida has also been advanced by the circumstance, that certain branchiferous worms bear their eggs about with them until the evolution of the young. Thus, in *Eunice sanguinea*, according to Koch, the young are brought to maturity in the cavity of the body of the mother, where they are retained until they reach a length of from one to two inches, and acquire from 100 to 120 segments. No trace of cilia appears to exist in these young animals. The progeny of *Nereis diversicolor* quit the cavity of the mother at a much earlier stage of development. In female specimens of this Annelide taken in April on the coast near Greifswald, where it is very abundant, I observed that the oval or pyriform embryos, which are uniformly covered with cilia, and, from their reddish-yellow colour, remind one of the young of *Medusa aurita*, came in hundreds out of small apertures on the sides of the body, under the pedal tubercles. These embryos (Pl. II. figs. 11 & 12), which swim about rapidly, measure $\frac{1}{10}$ th to $\frac{1}{8}$ th of a line; they are rather opaque, in consequence of the numerous fatty vitelline granules imbedded in the body. They swim with the narrow end forwards, and the little animal constantly turns on its axis. Near the anterior extremity is the mouth, marked out by longer cilia arranged in a circle, and from this a canal passes inwards, the hinder extremity of which did not appear to be formed. In front of the mouth there are one or two dark eye-spots, without refractive bodies. I did not observe any further metamorphosis, as the larvæ soon died in my glasses.

Instead of the cavity of the body, the embryos of other Annelida are developed in peculiar sacs situated on the dorsal or ventral surface of the mother, where they generally attain a proportionably high development. This is the case in *Sacconereis*†,

* Jahresbericht, 1848-53, and Wiegmann's Archiv, 1855, i. p. 21. See Annals, 2nd Series, xvi. p. 264.

† *Sacconereis helgolandica* has recently been ascertained by Krolm (Müller's Archiv, 1855, p. 439) to be the result of the division of *Autolytus prolifer*, a great step in the history of the development of this interesting

according to the observations of Johann and Max Müller, and of myself, in *Cystonereis*, Kölliker, *Exogene*, Oersted and Kölliker, and *Syllis pulligera*, Krohn. In *Sacconereis* the young appear to issue in swarms from the ventral sacs of the mother, as they are provided with several bands of cilia, and when the sac is artificially destroyed, possess the power of swimming in a high degree; whilst the evolution of the young of *Cystonereis*, *Exogene*, and *Syllis pulligera* takes place on the body of the mother until the disappearance of the cilia (which are certainly present in the earliest stages of *Exogene cirrata* and *Syllis pulligera*) and the appearance of the segments and lateral bristles.

In a considerable number of Branchiferous Annelides, again, the eggs are deposited enclosed in a mass of jelly, and develop themselves in this covering, without any connexion with the mother, until the young are furnished with bristles and other locomotive organs like those of the mature animals. These do not enable them to swim freely for any length of time, but only to creep along the sea bottom. Examples of this kind occur in the Tubicular families of the *Terebellacea* and *Serpulacea* in the genera *Terebella* and *Protula*, with whose young Milne-Edwards has made us acquainted. As the masses of eggs of these animals are attached to the exterior of their tubes, no doubt can exist as to their origin, when they are collected at the same time with the mother; and the tracing of their further development is extraordinarily facilitated by the fact that they require no change of water, at least as long as they remain enclosed in the gelatinous masses, and therefore survive in the glasses.

An example of this mode of development is also presented by *Arenicola piscatorum*, the egg-masses of which I collected near Cuxhaven, on the 22nd March 1852, and brought with me to Greifswald, where the further development took place. On the island of Neuwerk, which lies a few miles to seaward of Cuxhaven, the traces of *Arenicola piscatorum* occur in extraordinary numbers. In passing, during the ebb-tide, over a surface of sand but slightly covered with water, I saw, lying on the sand, close to almost every one of the little heaps thrown up by the worms

gemmaiparous worm; and the same is probably the case with the second species, *S. Schultzei*, from the Mediterranean, described by J. Müller. I have no doubt that the animal of this genus taken by me at Heligoland, and mentioned by J. Müller from my letters, is identical with that observed by Max Müller (Müller's Archiv, 1855, p. 13). I took no notes of the number of segments in the body; but the young animal is represented at fig. 10 (Pl. II.). It represents a further step in the development of the young worm represented by M. Müller, l. c. tab. 2. figs. 5-8, and is particularly distinguished by its four bands of cilia. Of the fine cilia which at an earlier period covered the whole body, only those on the head are still in existence.

at this period, which were here scarcely six inches apart, a pyriform gelatinous mass about half an inch long and of a fine rose colour. On examining them more closely, I found that each of them was fastened into the sand by a gelatinous stem of about two inches long, and that the red colour was caused by an aggregation of red granules in the interior of the greenish-yellow jelly. These are the eggs of *Arenicola*, of which from 300 to 400 are enclosed in the gelatinous mucus (Pl. II. fig. 1).

From microscopic examination of some of them, it appeared that the yolks lay close together in the gelatinous mass, only enclosed in an extremely delicate vitelline membrane, something like those of *Nemertes* in their pyriform vesicles; and as I found no traces of the commencement of segmentation, I concluded that the eggs were only just deposited.

Unfortunately I was unable to trace their development on the spot, and only recommenced my observations nine days afterwards on the egg-masses which I took with me to Greifswald. I then found that the process of segmentation was completed in most cases, and that the oval embryos had acquired a fringe of extremely fine cilia, in the form of a broad band, near what I afterwards ascertained to be the anterior extremity (fig. 2). Other eggs, which were rather backward in their development, although they certainly gave no satisfactory clue to the course of the process of segmentation, showed at all events that this was complete, and that the vitelline membrane had taken part in it so far as to furnish envelopes for the globules of segmentation, and consequently gave off the materials for the walls of the embryonal cells. The embryos could therefore have been enveloped in no other capsule, but lay quite free in the semifluid jelly, in which they began to move about slowly after the development of the cilia. The animals soon became rather more elongated (fig. 3), and with this change of form new circles of cilia made their appearance (fig. 4), one close before and a second close behind the first ciliary band, and a third at the hinder extremity of the body. All three of these are very narrow, and consist only of a few series of very fine cilia, which can only be seen with a high magnifying power, and never exhibit the rotatory motion which is often so remarkable in the free-swimming Annelidan larvæ. At the same time two dark-red eye-spots made their appearance in the neighbourhood of the first circle of cilia. This was the condition of the embryos on the twelfth day.

The length of the animal now gradually increases, whilst the circles of cilia undergo no change in number or form. On the other hand, distinct annular constrictions make their appearance in the middle of the body, the first close behind the last circle of

cilia, whilst the following ones are at first rather close together (fig. 5), but gradually become more distant with the further growth of the animal (fig. 6). The body, which hitherto had been quite opaque, now separated into a lighter peripheric portion, lying under the skin, which still continued rather dark, and an opaque central portion. The former represents the cavity of the body, the latter the intestine, in which a cavity may be recognized by the granules which move about in it. The intestinal canal does not, however, lie free in the general cavity, but is attached to the inner surface of the skin by annular bands corresponding in number with the developed segments of the body. A mouth exists behind the eyes, on the ventral surface; the anal opening occupies the extreme hinder end of the body. No traces of a nervous or vascular system are perceptible.

On the twentieth to the twenty-fourth day the bands of cilia disappear entirely, and the young animals, which had previously moved slowly about in the gelatinous mass, now quit it in the form of sluggish, helpless worms. Their length is now $\frac{1}{2}$ to $\frac{3}{4}$ ''' . Their form is cylindrical, somewhat widened towards the anterior extremity, which terminates in a point, and truncated behind (fig. 7). The mouth lies close behind the red eye-spots, which are destitute of a refractive medium; it leads into a muscular œsophagus (*a*), and this into the intestine, which runs straight backwards to the anus. The number of segments in the body has increased to 10 or 12 by additions at the hinder extremity (between the last and penultimate segments). On the most anterior of these the first lateral bristles are perceptible, standing in groups of from two to four; they are delicately serrated on one edge (fig. 9), in this respect resembling the infinitely larger bristles of the mature *Arenicola*.

My endeavours to keep these young worms any longer failed entirely. I put them into a glass upon a thin stratum of sand which I had brought with me from the island of Neuwerk, containing a variety of Infusoria and Algæ which might possibly have served them for nourishment, but they died without undergoing any further change of form. I think, however, that I saw indications of the formation of the auditory vesicle, as I observed on each side, in front of the eyes, a small vesicle with a tolerably sharp outline, and with irregularly granular, but not calcareous, contents, which would probably afterwards be the otolithes.

It is to be expected that the young *Arenicolæ*, after creeping out of their gelatinous envelope, would bore into the sand in the neighbourhood of their parents, and then gradually acquire their mature form. The next thing to be done, therefore, is to seek the young in this situation at the proper season.

From the foregoing statements, the development of *Arenicola* has the greatest similarity with that observed by Milne-Edwards in *Terebella* and *Protula*. In these, also, the eggs are deposited without any envelope besides the vitelline membrane in gelatinous masses, in which the young are developed to a certain point. They also obtain an anterior and posterior circle of cilia, by means of which they move about in the soft jelly, and do not quit this until their more powerful locomotive organs, the bristles, are developed, and the cilia have disappeared, so that a free swimming condition does not occur. Nevertheless there is a difference in the number of bands of cilia, as the last-mentioned forms do not acquire the two fine circles which occur in *Arenicola* before and behind the broad band. But no great stress can be laid upon this difference, as the increased number of ciliary circles appears in this case to be rather a division of the original simple anterior band, and they are all situated upon the same segment, the head. Milne-Edwards supposes that the young animals, after the development of the first cilia upon their surface, creep out of the vitelline membrane, which is afterwards absorbed. It appears to me more probable, that in *Terebella* and *Protula*, as in *Arenicola*, the vitelline membrane passes into the embryo itself, by furnishing the envelopes of the globules of segmentation, or the future embryonal cells, and that consequently no egg-capsule exists from which the embryos must escape. Milne-Edwards did not observe the process of segmentation, and was consequently in uncertainty as to the part taken in it by the vitelline membrane.

Remak, in his recent investigations upon the development of the Vertebrata, has described the part played by the vitelline membrane, which he calls the *egg-cell-membrane* (*Eizellenmembran*), in the segmentation of the egg of the Frog, as consisting in its furnishing envelopes for the segmentary divisions by the agency of constrictions, which it acquires simultaneously with the vitelline mass itself. I have confirmed this statement in the eggs of *Petromyzon Planeri*, which also undergo a total segmentation*. I doubt, however, the propriety of adopting the name of egg-cell-membrane for the membrane immediately enveloping the yolk, as this and no other deserves the name of vitelline membrane. I believe we must regard the vitelline membrane as having the same signification in the eggs of *Arenicola* as in these eggs.

In other Branchiferous Annelides, however, the behaviour of the membranes of the egg appears to be different. At least in the case of *Hermella*, Quatrefages asserts that during segmenta-

* See Annals, May 1856, p. 443.

tion the vitelline membrane retains its form of a simple vesicle, but afterwards unites with the surface of the embryonal cells, forming the skin of the embryo, and acquiring cilia on its outer surface. And this statement acquires more force from those of O. Schmidt with regard to the development of *Amphicora* (*Fabricia*) *sabella**. This little Annelide, which has been classed amongst the Cephalobranchiate worms, although, according to Schmidt, it bears its branchiæ on its tail, lays its eggs in the tube which it inhabits, but which it then quits. Their development resembles that of *Exogene* and *Cystonereis*, and in the course of it the vitelline membrane becomes converted into the skin of the embryo, as in *Hermella*. New observations must prove the reality of the occurrence of such a participation of an egg-capsule in the formation of the embryo, which would differ from all known modes of animal development.

If we attempt, in conclusion, to refer the numerous and variously formed Annelidan larvæ hitherto observed to a few typical forms, in order to facilitate the examination of their further metamorphoses, and acquire an approximate knowledge of the mode of development common to all, the nature of the ciliary coat, and the number and arrangement of the bands of cilia when such occur, present us with a constant character applicable to this purpose, as has already been pointed out by others.

In this way Busch† distinguishes two groups of Annelidan larvæ,—one, for which Lovén's larva‡ serves as the type, *possessing a circlet of cilia at each end of the body* (the anterior generally situated between the eyes and the mouth), *between which the segments of the worm are afterwards developed*. These have been subsequently named *Telotrochæ* by J. Müller (Archiv, 1855, p. 12); and besides Lovén's larva, the destiny of which is unknown, this series includes a portion of Busch's larvæ, which also cannot be referred to their parents, the larvæ of *Polynoë* (Sars), *Nereis* (Busch, l. c. tab. 9. fig. 11), *Terebella*, *Protula*, and *Arenicola*. Perhaps also the young *Hermellæ* may be referred to this position, as Quatrefages thinks (Ann. des Sc. Nat. 3 sér. x. p. 189), although, according to the description and figure, they are destitute of a hinder circle of cilia.

The second group established by Busch is that of the *Mesotrochæ*, *with a simple or double wheel-like organ situated in the middle of the body*. To this belong all the larvæ to which the generic name of *Mesotrocha* has been applied, one of which, the *M. sexoculata*, as already stated, is now ascertained to be the young state of a *Chaetopterus*.

* Neue Beiträge zur Naturgeschichte der Würmer, p. 29.

† Beobachtungen, &c., pp. 57, 62.

‡ Wiegmann's Archiv, 1842, p. 302.

All Annelidan larvæ, however, cannot be referred to these divisions. For instance, the young of *Sacconereis*, as already mentioned, possess several (four) bands of cilia at equal distances on the body. The same is the case with a larva from Trieste, described by J. Müller (Monatsber. der Berl. Akad. 1851, p. 471); it measured $\frac{2}{10}'''$, and possessed no bristles, but was distinguished by the presence of bacillar corpuscles, like those in the skin of the *Turbellaria*; and also with the larva from Trieste with 2 strong and 10-14 weaker circles of cilia, figured by Busch, tab. 9. figs. 9 and 10, which was traced further by Max Müller (Diss. Inaug. Berol. 1852, p. 25, tab. 3. figs. 14-17), but without arriving at its definite form. These young Annelida may be denominated *Polytrochæ*, after J. Müller.

Lastly, the general coating of cilia, which frequently occurs in the earliest period of embryonic life (*Chaetopterus*, *Sacconereis*, *Nereis diversicolor*), but generally gives place to the isolated circles, appears to be persistent in the same form throughout the whole larval existence of many Annelides. For such J. Müller proposed the name of *Atrochæ*; he observed one of them at Trieste, measuring $\frac{1}{10}'''$, which was already furnished with developed setæ (Monatsber. 1851, p. 472).

All the young Annelides referred to these four divisions agree in their development from the egg in the form of globular or oval, *non-annulated* embryos, in receiving indications of division into segments from the circlets of cilia when these are present, but only acquiring the form of an Annelide, with distinct body-segments and lateral bristles, after the lapse of some time. A considerable deviation from this plan of development is presented by *Cystonereis Edwardsii*, and *Exogene Oerstedii* and *cirrata*, described by Kölliker, as also by *Exogene naidina* according to Oersted, and *Amphicora sabella* according to O. Schmidt. The young of these animals acquire, whilst still in the egg, a form similar to that of the mother, as they appear at their first formation divided into several segments, like the embryos of the Articulata. In the embryos of *Cystonereis Edwardsii*, Kölliker counted 8-9 segments, and 6 in *Exogene cirrata*. In these there are no traces of circles of cilia, and even a general coat of cilia is wanting; whilst, on the other hand, fine cilia occur on certain regions of the body, as in the embryo of *Exogene cirrata* on the ventral surface. In these animals, therefore, we cannot speak of a larval state, as they pass through all those changes of form whilst still in the egg, which gradually occur in the others during their free-swimming period, and long after their embryonal existence. They are therefore destitute of the provisional, transitory organs which characterize the larval condition of the others.

To this short summary of the present state of our knowledge

of the development of the Branchiferous Annelides, I add a tabular view, in families, genera and species, of all those worms whose earlier states have hitherto been observed, whether singly or in complete series. The systematic arrangement is that of Grube, in his 'Familien der Anneliden.' It shows how extremely small, in comparison with the number of known species, is that of the observations of their developmental forms, a number however which would certainly be doubled, if we were acquainted with the parentage of all the larvæ hitherto observed.

Tabular View of those Branchiferous Annelides of which the Young States have already been observed.

Rapacia.

APHRODITEA ..	<i>Polynoë cirrata</i>	Sars, Wieg. Arch. 1845, i. p. 11.
	<i>Polynoë</i>	M. Müller, Arch. 1851, p. 323; Desor, Bost. Journ. vi. p. 12.
EUNICEA	<i>Eunice sanguinea</i>	Koch, Neue Denkschr. der schweiz. Gesellsch. viii.
LYCORIDEA ..	<i>Nereis diversicolor</i> ..	Schultze, in this paper.
	<i>Nereis</i> , sp. dub.,	Milne-Edwards, Annales des Sci. Nat. 3 sér. iii. p. 166; Busch, Beobachtungen, &c. p. 69. tab. 9. figs. 11, 12.
PHYLLODOCEA.	<i>Phyllodoce</i> , sp.	M. Müller, Arch. 1855, p. 17, note.
SYLLIDEA	<i>Syllis pulligera</i>	Krohn, Wieg. Arch. 1852, i. p. 251.
	<i>Autolytus prolifer</i>	Krohn, Wieg. Arch. 1822, i. p. 66; Müller, Arch. 1855, p. 489.
	(<i>Sacconereis helgolandica</i> .)	M. Müller, Müll. Arch. 1855, p. 13; Schultze, in this paper.
	<i>Sacconereis Schultzei</i> .)	J. Müller, Ueber den allgem. Plan. in der Entwicklung der Echinodermen, p. 7, note.
	<i>Cystonereis Edwardsii</i> .	Kölliker, in Koch, Neue Denkschr. der schweiz. Gesellsch. viii. p. 21.
	<i>Exogene naidina</i>	Oersted, Wieg. Arch. 1845, p. 20.
	<i>Exogene Oerstedii</i> and <i>cirrata</i> .	Kölliker, Neue Denkschr. der schweiz. Gesellsch. viii. pp. 15, 22.
ARICIEA	<i>Nerine (Malacoceros) longirostris</i> .	Leuckart*, Wieg. Arch. 1855, i. pp. 63 & 77; Busch, Beob. tab. 8. figs. 1-4.
	<i>Leucodore ciliata</i>	Oersted, Annul. Dan. Consp. p. 39. tab. 6. fig. 96 (?); Frey and Leuckart, Beiträge, &c. p. 98. tab. 1. fig. 19 (?).

* See Annals, 2nd Series, xvi. p. 299.

Limivora.

TELETHUSA ..	<i>Arenicola piscatorum.</i>	Schultze, in this paper.
TEREBELLACEA.	<i>Terebella nebulosa</i> , &c.	Milne-Edwards, Ann. des Sci. Nat. 3 sér. iii. p. 145.
HERMELLACEA.	<i>Hermella</i>	Quatrefages, Ann. des Sci. Nat. 3 sér. x. p. 153.
SERPULACEA..	<i>Protula</i>	Milne-Edwards, Ann. des Sci. Nat. 3 sér. iii. p. 161.
	<i>Fabricia (Amphicora) sabella.</i>	O. Schmidt, Neue Beitr. zur Naturgesch. der Würmer, 1848, p. 27.
CHÆTOPTEREA.	<i>Chætopterus</i>	M. Müller, Arch. 1855, p. 1. <i>Mesotrocha sexoculata</i> , J. Müller, Arch. 1846, p. 101; Busch, Müll. Arch. 1847, p. 187; Beob. &c. 1851, p. 59.

EXPLANATION OF PLATE II.

- Fig. 1.* Mass of eggs of *Arenicola piscatorum*, enclosed in a pedunculate gelatinous envelope: natural size.
- Fig. 2.* Embryo of *Arenicola* after the process of segmentation has reached the stage in which the embryo commences its movements in the gelatinous mass by means of a broad band of cilia at the anterior end (about 10 days old). 150 diameters.
- Fig. 3.* The same embryo, rather more elongated (one day older).
- Fig. 4.* An embryo in which the body has become more elongated, with the appearance of new bands of cilia (12 days old).
- Fig. 5.* An embryo, in the interior of which the differentiation of the central cord (the alimentary canal) has commenced, with the appearance of the first traces of segments (13 days).
- Fig. 6.* An embryo in which the intestinal canal and the segments are still more distinctly developed; the general cavity is traversed by transverse walls, corresponding in number with the segments, and attaching the intestine to the inner surface of the walls of the body: the circles of cilia are still unaltered (17 days).
- Fig. 7.* A young larva, 24 days old, which has escaped from the gelatinous envelope. The circlets of cilia have disappeared, the number of segments has considerably increased, and the anterior extremity of the intestine passes into a barrel-shaped œsophagus, the wide anterior opening of which is close to the mouth (*a*). The anterior segments of the body are furnished with setæ. 80 diam.
- Fig. 8.* Anterior extremity of the same embryo, seen from the side to show the position of the mouth on the ventral surface.
- Fig. 9.* Setæ from the anterior segments of the body. 400 diam.
- Fig. 10.* Young of *Sacconereis*, with four circles of cilia, from Helligoland.
- Figs. 11 & 12.* Young of *Nereis diversicolor*, just escaped from the cavity of the mother; fig. 11, from the ventral side, showing the mouth, *a*; fig. 12, from the back.